

Impact of climate change on potential habitat distribution of Sciaenidae in the coastal waters of China

Wen Yang^{1, 2}, Wenjia Hu^{1, 3, 4}, Bin Chen^{1, 3, 4}, Hongjian Tan¹, Shangke Su¹, Like Ding^{1, 2}, Peng Dong⁵, Weiwei Yu^{1, 3, 4}, Jianguo Du^{1, 3, 4*}

¹Third Institute of Oceanography, Ministry of Natural Resources, Xiamen 361005, China

²College of Marine Science, Shanghai Ocean University, Shanghai 201306, China

³Key Laboratory of Marine Ecological Conservation and Restoration, Ministry of Natural Resources, Xiamen 361005, China

⁴Fujian Provincial Key Laboratory of Marine Ecological Conservation and Restoration, Xiamen 361005, China

⁵Aerospace Information Research Institute, Chinese Academy of Sciences, Beijing 100094, China

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Abstract

Climate change has affected and will continue to affect the spatial distribution patterns of marine organisms. To understand the impact of climate change on the distribution patterns and species richness of the Sciaenidae in China's coastal waters, the maximum entropy model was used to combine six environmental factors and predict the potential distribution of 12 major species of Sciaenidae by 2050s under Representative Concentration Pathways (RCPs) 2.6 and 8.5. The results showed that the average area under the receiver operating characteristic curve of the model was 0.917, indicating that the model predictions were accurate and reliable. The main driving factors affecting the potential distribution of these fishes were dissolved oxygen, salinity, and sea surface temperature (SST). There was an overall northward shift in the potential habitat areas of these fishes under the two climate scenarios. The total potential habitat areas of *Larimichthys polyactis*, *Pennahia argentata*, and *Pennahia pawak* decreased under both climate scenarios, while the total habitat area of *Johnius belengerii*, *Pennahia anea*, *Miichthys miiuy*, *Collichthys lucidus*, and *Collichthys niveatus* increased, suggesting that these might be loser and winner species, respectively. The expansion rate, contraction rate, degree of centroid change, and species richness in the potential habitats were generally more significant under RCP8.5 than RCP2.6. The mean shift rates of the potential distribution were 41.50 km/(10 a) and 29.20 km/(10 a) under RCP8.5 and RCP2.6, respectively. The changes in Sciaenidae species richness under climate change were bounded by the Changjiang River Estuary waters, with obvious north-south differences. Some waters with increased species richness may become refuges for Sciaenidae fishes under climate change. The richness and habitat area change rate of some aquatic germplasm resources will decrease, meanings that these reserves are more sensitive to climate change, and more attention should be paid to the potential challenges and opportunities for fishery managers. This study may provide a scientific basis for the management and conservation of Sciaenidae in China under climate change.

Key words: climate change, Sciaenidae, potential distribution, species richness, habitat

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1 Introduction

Global climate change and human activities have direct or indirect impacts on both terrestrial and marine ecosystems, and in particular, distribution studies concerning to climate change have attracted widespread attention (Pachauri et al., 2014; Burrows et al., 2011; Tan et al., 2020; Yao and Somero, 2014). The global marine environment has already changed under climate change, including sea surface temperature (SST), salinity, and dissolved oxygen concentration, (Bindoff et al., 2019). It has been shown that climate change can lead to changes in phenology and marine community structure (Bindoff et al., 2019; Jones and Ch-

eung, 2015; Wang et al., 2019; Du et al., 2012; Yuan et al., 2017). In general, warming triggers a polar shift in the distribution of marine organisms, leading to a decline in fish species richness in tropical waters, high potential for species invasion in mid- and high-latitude waters, and a global turnover of fish species that may lead to numerous local extinctions (Cheung et al., 2015; Jones and Cheung, 2015; Lotze et al., 2019). However, changes in species distribution also vary according to specific sea areas and species (Morley et al., 2018; Zhu et al., 2020). At the regional scale, most studies have focused on the North Atlantic Ocean, while the Northwest Pacific and Indian Ocean have received the

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*Corresponding author, E-mail: dujianguo@tio.org.cn

least attention (Lenoir et al., 2011; Yu et al., 2013; Melo-Merino et al., 2020). In addition, in recent years, there has been a growing number of national-scale studies on the effects of climate change on marine fishes, including those in Canada (Andrews et al., 2020), the United States (Petatán-Ramírez et al., 2020), and other regions. China's coastal waters are the main habitats of many important economic fish species worldwide. China is also one of the main contributors the most to global fishery production. It has extremely rich marine biodiversity, but it also faces damage to the health of the marine ecological environment and the rapid decline of biodiversity under the influence of climate change (Kang et al., 2021). It is of great significance to explore the impact of climate change in China's coastal waters on suitable fish habitats, the protection of fish biodiversity in China, and the maintenance of global marine biodiversity. Although climate change has been known to cause decreases in the distribution areas of many marine species in East Asia (Yu et al., 2013; Zhang et al., 2019), there have been far fewer studies in China than in Europe, North America, and South Pacific countries (Zhu et al., 2020; Zhang, 2020; Zhang et al., 2020a). Therefore, understanding the changes in the spatial and temporal distribution of marine fish habitats in China under the influence of climate is of great significance for the future conservation and management of marine fish in China.

Sciaenidae fishes have a wide global distribution and most of them are considered as important marine fish species because of their high economic value. Most species in the family are important marine economic fish species in China; among them, the yellow croaker and large yellow croaker are endemic to the China seas and are among the three traditional marine economic fish species in China (Liu, 2008; Xie et al., 2012). Large scale investigations on Sciaenidae are costly and relatively inefficient, and this causes a substantial lack of the information required for relative studies (Xu and Chen, 2010; Xie et al., 2012). Climate change will have a significant impact on the resources and distribution of Sciaenidae, which are highly abundant and distributed in offshore areas (Liu et al., 2017; Wang et al., 2019; Yuan et al., 2017). In this study, species distribution models combined with two climate scenarios were used to investigate the potential distribution of the Sciaenidae. Such models, can avoid the low time efficiency of traditional survey methods and provide reliable predictions of fish distributions in the future.

Species distribution models (SDMs) are used to predict the distribution of species by studying the relationship between species and their associated environmental factors, and they provide a simple and effective way to predict the distribution of species habitats (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000; Kumar et al., 2014; Liang et al., 2021). Common SDMs include the maximum entropy model (MaxEnt), boosted regression tree model, random forest model, generalized linear model, and generalized additive model, of which the MaxEnt model is the most commonly used in research (Melo-Merino et al., 2020). Many international studies have used SDMs to predict fish migration under the influence of climate change. For example, one study used a MaxEnt model to predict significant changes in the spatial patterns of habitat suitability for anchovy in South American waters under four climate scenarios, and most of the original habitats will no longer be suitable for their survival under climate change (Silva et al., 2019). In addition to global scale search, studies on shifts in the distributions of marine fish have mainly focused on the North American continental shelf waters, the North Pacific offshore waters, the South Atlantic, etc. (Cheung et al., 2009; Cheung et al., 2015; Morley et al., 2018; Silva et al.,

2019). However, there are relatively few relevant studies in China, and the only studies on climate impacts on fish distribution shifts have focused on pelagic fishing grounds or areas concentrated in the Yellow Sea and the Changjiang River Estuary (Zhu et al., 2020; Zhang et al., 2020b); national-scale studies are limited to a single species of fish (Wang et al., 2021).

In this study, the MaxEnt model was used to investigate changes in the distributions of 12 species of Sciaenidae (*Larimichthys crocea*, *Larimichthys polyactis*, *Johnius grypotus*, *Johnius belengerii*, *Nibea albiflora*, *Pennahia argentata*, *Pennahia pawak*, *Pennahia macrocephalus*, *Pennahia anea*, *Collichthys niveatus*, *Collichthys lucidus*, and *Miichthys miiuy*) in the coastal waters of China under two Representative Concentration Pathways (RCPs) climate change scenarios (RCP2.6 and RCP8.5) by 2050s. This study investigated the shift changes and extent of the potential distribution of Sciaenidae, predicted the future spatial distribution of Sciaenidae in China's coastal waters, and analyzed the changes in their habitats. The results will provide a scientific basis for the conservation and management of Sciaenidae in China, as well as a useful reference for future studies on the potential distribution of other marine fishes in China under climate change.

2 Materials and methods

2.1 Overview of the study area and collection of species distribution points

The study area (Fig. 1) covers the offshore area of China, from the Liaodong Bay in the north to Hainan Island in the south. It spans 24 latitudes (approximately 17°–41°N) and 17 longitudes (approximately 107°–124°E), and contains the main distribution areas of the selected species of Sciaenidae in China (Chen et al., 2021a; Pei et al., 2021; Shen et al., 2020). Fish distribution latitude and longitude data were obtained from the spatial and temporal distribution data of the Chinese Offshore Investigation and Assessment project and global biogeographic databases. The survey covered the Bohai Sea, Yellow Sea, East China Sea, and South China Sea, and was conducted in the spring, summer, autumn, and winter seasons of 2004–2009. The biological voyages conducted trawl surveys, the trawling time was 1 h per station, and the speed was controlled at approximately 3 kn (Chinese Offshore Investigation and Assessment Project Office of the State Oceanic Administration, 2006; State Oceanic Administration, 2016). Occurrence data from global biogeographic databases, such as the Global Biodiversity Information Facility (GBIF, www.gbif.org), Ocean Biodiversity Information Systems (OBIS, www.iobis.org), and Fishbase (FishBase, www.fishbase.org), were also collected. All occurrence records were collated, duplicated sites were removed, and spatial rarefying was implemented using ENMTools to reduce the sampling deviation caused by the cluster effect. Finally, 1 756 fish distribution occurrence records from 12 fish species were collected as inputs for the model (Table 1).

2.2 Environmental data preparation

The types of environmental factors used in species distribution models for fish distribution prediction included physico-chemical factors, hydrological factors, habitat types, and substrate types. The variables commonly used in marine fish distribution studies are sea surface temperature, salinity, and currents (Melo-Merino et al., 2020; Silva et al., 2019; Wang et al., 2021). In this study, sea surface temperature, salinity, dissolved oxygen, current velocity, water depth, and distance from the shore were selected as environmental factors for model prediction; bathy-

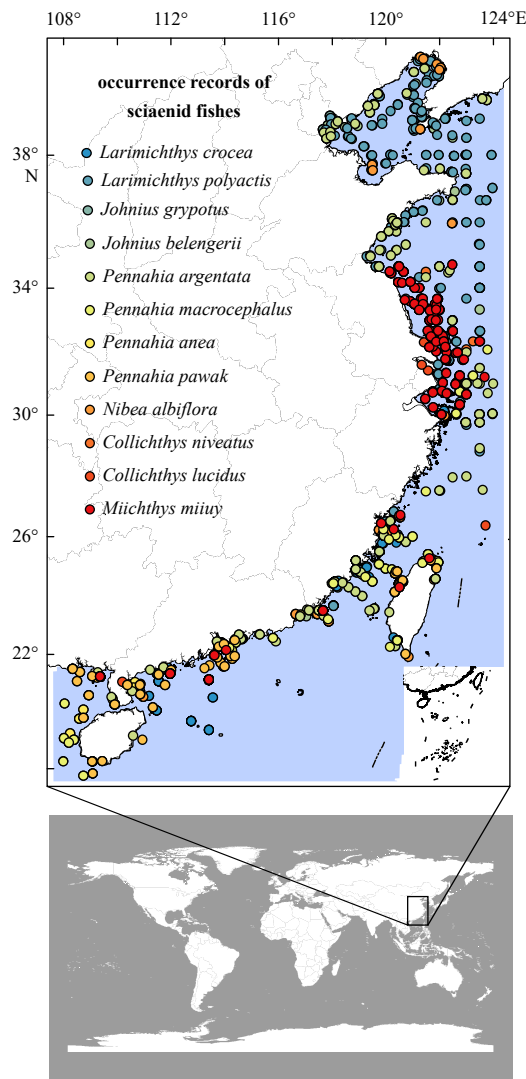


Fig. 1. Study area and occurrence records of 12 Sciaenidae species in the coastal waters of China.

metry and distance from land were stable variables, and the remaining were variables. The environmental data sources are shown in Table 2, and the highest and lowest representative concentration pathway discharge scenarios RCP2.6 and RCP8.5, respectively, from the Coupled Model Intercomparison Projects (CMIP5) were chosen as the future climate projection scenarios

for predicting the fish distribution in 2050s. The future scenario data of sea surface temperature, salinity and dissolved oxygen were integrated with IPSL-CM5A-MR (Dufresne et al., 2013) global circulation model data and GFDL-ESM2M (Dunne et al., 2012) model data based on the bio-oracle dataset (Tyberghein et al., 2012; Assis et al., 2018). And the low-resolution raw data were de-biased using the change-factor downscaling method to obtain higher accuracy data, corrected for systematic offsets between modeled representations and observations of present climates, and fitted to the study area (Tabor and Williams, 2010). The resolution of the current and future climate environment datasets was processed uniformly to 1 km for the construction of the prediction model. The climate anomalies between the present and the 2050s were extracted from the data of two models and were resampled to resolution of 1 km. Using bilinear spatial interpolation added to the current data covering the same region to produce the downscaled climate model dataset (Tabor and Williams, 2010).

2.3 MaxEnt model construction and evaluation

In this study, MaxEnt model version 3.4.4 (Phillips and Dudík, 2008), was used to model the potential distribution of 12 species of Sciaenidae fish offshore of China. The model randomly selected 75% of the input fish distribution point data as the training set and modeled them with the corresponding current environmental factors to obtain the relationship between them, while the remaining 25% of the sample data are used as testing data. The established model was projected using the scenarios for current and future environmental variables. The types of environmental variables at the two time points needed to be consistent to construct the prediction models of the current and future distribution of the fish. The most important parameters affecting the model construction results are the feature combination and the regularization multiplier parameters, the model contains five feature types that can be combined: linear (L), quadratic (Q), hinge (H), product (P) and threshold (T) (Radosavljevic and Anderson, 2014). Different combinations of feature parameters were selected to debug the model, and the optimal combination was selected for modeling. In this study, in order to obtain the best model parameters for modelling, the default parameter settings of the model were adjusted using the ENMeval data package in R to filter the optimal combination of model feature parameters and regularization multipliers (Hu et al., 2022; Kass et al., 2021; Muscarella et al., 2020). In this study, five characteristic combination parameters ("L", "H", "LH", "LP", and "LHPT") were used to adjust the model, setting the regularization multipliers of the model parameters between 0.5 and 4, increasing by 0.5. The bootstrap resampling method was selected, and the average value

Table 1. Details of 12 fish species

Genus	Species	Survey data (2004–2009)	Global data in study area (2004–2009)
<i>Larimichthys</i>	<i>Larimichthys crocea</i>	183	39
<i>Larimichthys</i>	<i>Larimichthys polyactis</i>	401	10
<i>Nibea</i>	<i>Nibea albiflora</i>	77	2
<i>Johnius</i>	<i>Johnius grypotus</i>	34	2
<i>Johnius</i>	<i>Johnius belengerii</i>	182	5
<i>Pennahia</i>	<i>Pennahia argentata</i>	201	12
<i>Pennahia</i>	<i>Pennahia macrocephalus</i>	95	6
<i>Pennahia</i>	<i>Pennahia pawak</i>	76	13
<i>Pennahia</i>	<i>Pennahia anea</i>	120	43
<i>Collichthys</i>	<i>Collichthys niveatus</i>	35	2
<i>Collichthys</i>	<i>Collichthys lucidus</i>	196	11
<i>Müichthys</i>	<i>Müichthys miiuy</i>	156	1

Table 2. List of environmental variables for the maximum entropy (MaxEnt) model

Variable	Source (current scenario)	Source (future scenarios, 2050s)	Unit	Initial resolution
Sea surface temperature	NASA MODIS-Aqua L3 products	NASA MODIS-Aqua L3 products, IPSL: https://esgf-node.ipsl.upmc.fr/projects/cmip6-ipsl/ , GFDL: https://www.gfdl.noaa.gov/	°C	1 km
Salinity	www.bio-oracle.org	www.bio-oracle.org , IPSL: https://esgf-node.ipsl.upmc.fr/projects/cmip6-ipsl/ , GFDL: https://www.gfdl.noaa.gov/	–	10 km
Dissolved oxygen	www.bio-oracle.org	www.bio-oracle.org , IPSL: https://esgf-node.ipsl.upmc.fr/projects/cmip6-ipsl/ , GFDL: https://www.gfdl.noaa.gov/	mol/m ³	10 km
Current velocity	www.bio-oracle.org	www.bio-oracle.org	m/s	10 km
Bathymetry	www.noaa.gov/	https://www.noaa.gov/	m	2 km
Distance from land	www.globalfishingwatch.com	www.globalfishingwatch.com	m	1 km

after 10 replicates was used as the model prediction result. The output was a raster dataset with image element values in the 0–1 interval, where the image element values characterized the probability of a species surviving in the region, with higher values resulting in a higher probability of species presence. The area under the curve (AUC) values were used to assess the model accuracy, with values ranging from 0 to 1. Permutation importance was used to reflect the role of environmental factors in determining the distribution of fish habitat, and the higher the percentage, the greater the influence of the factor on the distribution of fish.

2.4 Analysis of the potential spatial distribution patterns of the Sciaenidae and their changes under different climate scenarios

We set probability thresholds based on existing distribution records and used the “Reclassify” tool in ArcGIS to divide the model prediction results into “0/1” binary maps to visualize the distribution characteristics and changes in potential fish habitat. The model predictions were processed using the SDMtoolbox developed in Python to explore the impact of climate change on fish distribution patterns (Brown, 2014). The binary maps can characterize the potential habitat of the species, and the spatial overlay of the binary maps of 12 fish species can analyze the change in species richness of Sciaenidae under the influence of climate change. By overlaying the national aquatic germplasm resource reserves, whose main conservation targets include Sciaenidae, we visualized the reserves with more stable species composition or greater increase in richness, determined the sea areas that can provide shelter for Sciaenidae, and proposed corresponding management recommendations. The distribution changes between binary SDM tools were used to visualize and quantify the changes in the species’ habitats, and the centroid change tool was used to statistically analyze the direction and rate of shifts in the fish habitats. The above methods and processing were performed using ArcMap 10.8 (Esri, USA). Binary species maps were overlayed for statistical analysis of changes in richness and future directions for conservation management were analyzed in relation to aquatic germplasm reserves.

3 Results

3.1 Model performance and the importance of environmental variables

The results of MaxEnt runs for 12 species of Sciaenidae showed that the model AUC values were all above 0.85 (Table 3) and the mean AUC value was 0.917, validating the high predictive accuracy of the model.

The permutation importance of the environmental variables for the Sciaenidae showed that different environmental variables have different levels of importance for different fish species (Fig. 2). Sea surface temperature (SST) had a greater effect on the

Table 3. The area under the curve (AUC) values of the maximum entropy (MaxEnt) models

Species	Mean value of AUC	Standard deviation
<i>Larimichthys crocea</i>	0.909	0.027
<i>Larimichthys polyactis</i>	0.898	0.012
<i>Johnius grypotus</i>	0.889	0.051
<i>Johnius belangerii</i>	0.894	0.018
<i>Pennahia anea</i>	0.967	0.012
<i>Pennahia argentata</i>	0.860	0.022
<i>Pennahia macrocephalus</i>	0.908	0.026
<i>Pennahia pawak</i>	0.964	0.012
<i>Nibea albiflora</i>	0.882	0.042
<i>Miichthys miiuy</i>	0.950	0.021
<i>Collichthys lucidus</i>	0.922	0.019
<i>Collichthys niveatus</i>	0.964	0.024

potential distribution of *L. polyactis* and *J. grypotus*; and salinity had an effect on the potential distributions of *J. belangerii*, *M. miiuy*, *C. lucidus*, and *C. niveatus*. Dissolved oxygen concentration had a great effect on the potential distribution of *L. crocea*, *P. pawak*, *P. macrocephalus*, and *P. anea*; and offshore distance had a decisive effect on the potential distribution of *P. argentata* and *N. albiflora*; while current velocity had a relatively small effect on the potential distribution of habitats suitable for Sciaenidae. The analysis of the percentage importance of the environmental variables showed that the distance from the shore had a certain influence on the potential distribution of Sciaenidae. The importance of SST for *L. polyactis* and *J. grypotus* exceeded 35%, the percentage importance of salinity for *J. belangerii* and *C. niveatus* exceeded 60%, and the percentage importance of dissolved oxygen concentration for six species of fish, including *L. crocea*, *P. macrocephalus*, and *P. anea* exceeded 20%. As water depth and distance from shore are stable variables with negligible short term changes, the determinants of the potential distribution of Sciaenidae under the influence of climate were dissolved oxygen, salinity, and SST, in that order.

3.2 Habitat suitability under current and future climate scenarios

In the current study, the 12 species of Sciaenidae were distributed in the offshore areas of China, and the areas with fitness probabilities less than 0.2 and between 0.2–0.3, 0.3–0.5 and 0.5–1.0 were designated as non-suitable, and low, medium, and high suitability habitats, respectively. The results showed that the Sciaenidae fish species were distributed in the coastal waters of China, and *J. grypotus*, *J. belangerii*, *P. argentata*, *N. albiflora*, *M. miiuy*, and *C. niveatus* were abundantly distributed in all the offshore areas of China. *Larimichthys crocea*, *P. macrocephalus*, *P. anea*, and *P. pawak* were mainly distributed in the offshore areas

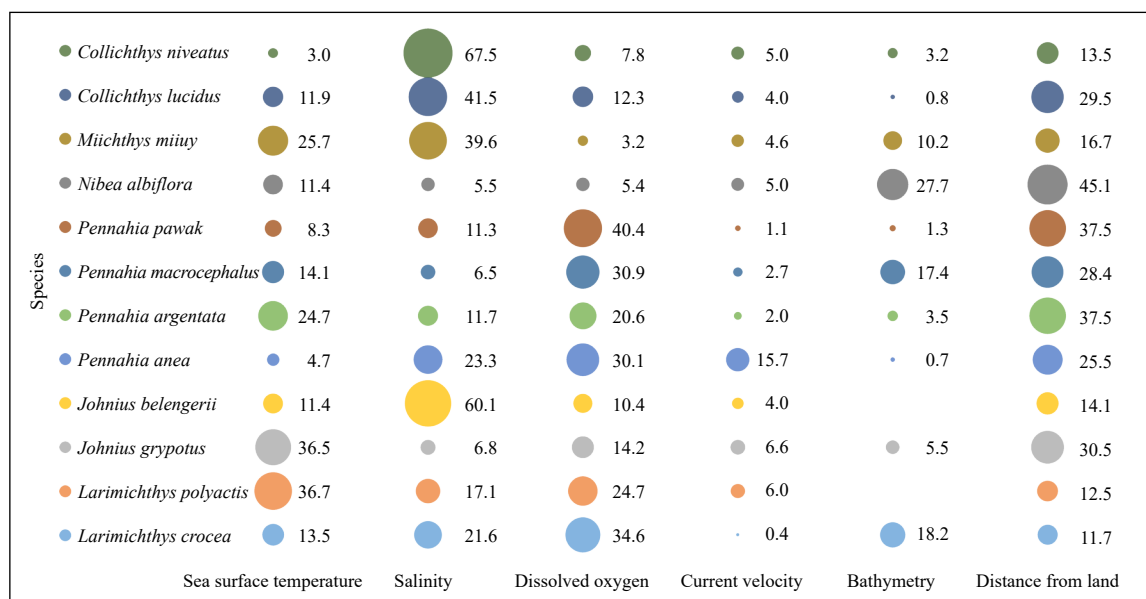


Fig. 2. Permutation importance of environment variables in sciaenidae distribution.

south of the Changjiang River Estuary; and *L. polyactis* and *C. niveatus* were mainly distributed in northern areas (Fig. 3). The high suitability habitats of all 12 species were concentrated in the coastal offshore area, and the outer edge of the high suitability habitats was distributed in the middle suitability habitats and low suitability habitats.

Under the RCP2.6 climate scenario, the potential distribution areas of the three habitat classes of fish changed, and the potential habitats of species with a nationwide offshore distribution, such as *J. grypotus*, tended to move northward as a whole. The northern boundaries of the potential habitats that are currently mainly distributed in southern waters, such as those of *L. crocea*, *P. macrocephalus*, and *P. pawak*, were predicted to migrate northward. Species that are mainly distributed in northern waters, such as *L. polyactis*, have a clear tendency to expand, and their southern boundaries may show some contraction. The distributions of the high suitability habitats of *L. polyactis*, *J. grypotus*, and *J. belangerii* expanded in the Bohai Sea. Under the RCP8.5 climate scenario, the trend of the potential habitats of fish was consistent with those under the RCP2.6 scenario, but the magnitude and extent of the change was more significant.

3.3 Analysis of geographical changes in habitats

The spatial distribution patterns of the potential habitats of the Sciaenidae species under the two climate scenarios, RCP2.6 and RCP8.5, are shown in Fig. 4. Compared with the current distributions, it was found that the boundary of the potential habitats for each species of fish has a certain degree of contraction or expansion under the climate change scenarios. The contraction area is mainly located at the southern edges of the suitable areas or close to the outer sea edge, and the expansion areas are mainly at the northern edges of the habitats or at the edges of the open sea. The total area, and the expansion, and contraction rates of the current and future potential habitats were calculated to show that *P. argentata* had the widest potential habitat and *C. niveatus* had the smallest potential habitat (Table 4). The fish species with decreases in their total potential habitats under both climate scenarios were *L. polyactis*, *P. argentata*, and *P. pawak*, possibly representing loser species. Increase changes in total area were observed for *J. belangerii*, *P. anea*, *M. miiuy*, *C. lucidus*, and *C.*

niveatus, which could represent winner species. Under the RCP2.6 climate scenario, *M. miiuy* had the greatest change in total potential habitat and the highest expansion rate (64.70%), while *P. macrocephalus* showed the highest potential habitat contraction rate (34.18%). Under the RCP8.5 scenario, *C. niveatus* showed the greatest change in total potential habitat and the highest expansion rate (86.55%), while the highest potential habitat contraction rate (47.03%) was observed for *P. pawak*; the general expansion and contraction rates of the Sciaenidae habitats were higher than those under the RCP2.6 climate scenario.

The changes in the spatial distribution patterns of the 12 fish species were reflected in the shift rates of the cores of their potential habitat distributions. The results are listed in Table 5. Under climate change, the centroids of the potential Sciaenidae habitat distributions all migrated northward; the number of centroids that migrated latitudinally was greater, and the shift distances were longer under the RCP8.5 climate scenario than under the RCP2.6 scenario. The latitudinal shift distances of the centroids of the potential Sciaenidae distributions under the RCP2.6 scenario ranged from 38.07 km to 305.25 km, with an average latitudinal centroid migration of 1.07°, a mean shift distance of 128.47 km, and a mean shift rate of 29.20 km/(10 a). The lowest shift rate was observed for *P. anea* and the highest (69.38 km/(10 a)) for *C. lucidus*. The latitudinal shift of the centroids of the Sciaenidae potential distributions under the RCP8.5 scenario ranged from 68.30 km to 419.08 km, with a mean latitudinal centroid shift of 1.40°, an average shift distance of 182.60 km, and an average shift rate of 41.50 km/(10 a), which are significantly greater than the shift rates and distances under the RCP2.6 scenario. The lowest shift rate was that of *C. niveatus*, and the highest was that of *C. lucidus* at 95.25 km/(10 a). The shift rates of *P. argentata*, *N. albiflora*, *M. miiuy*, and *C. lucidus* exceeded the average shift rates of Sciaenidae in both climate scenarios (Fig. 5).

3.4 Changes in the distribution of species richness of Sciaenidae

Under the future climate scenarios, the species richness of Sciaenidae varied significantly from north to south, with the Changjiang River Estuary as the boundary (Fig. 6). In the RCP2.6 scenario, the species richness of Sciaenidae decreased significantly in the Beibu Gulf, the waters around Hainan Island, the

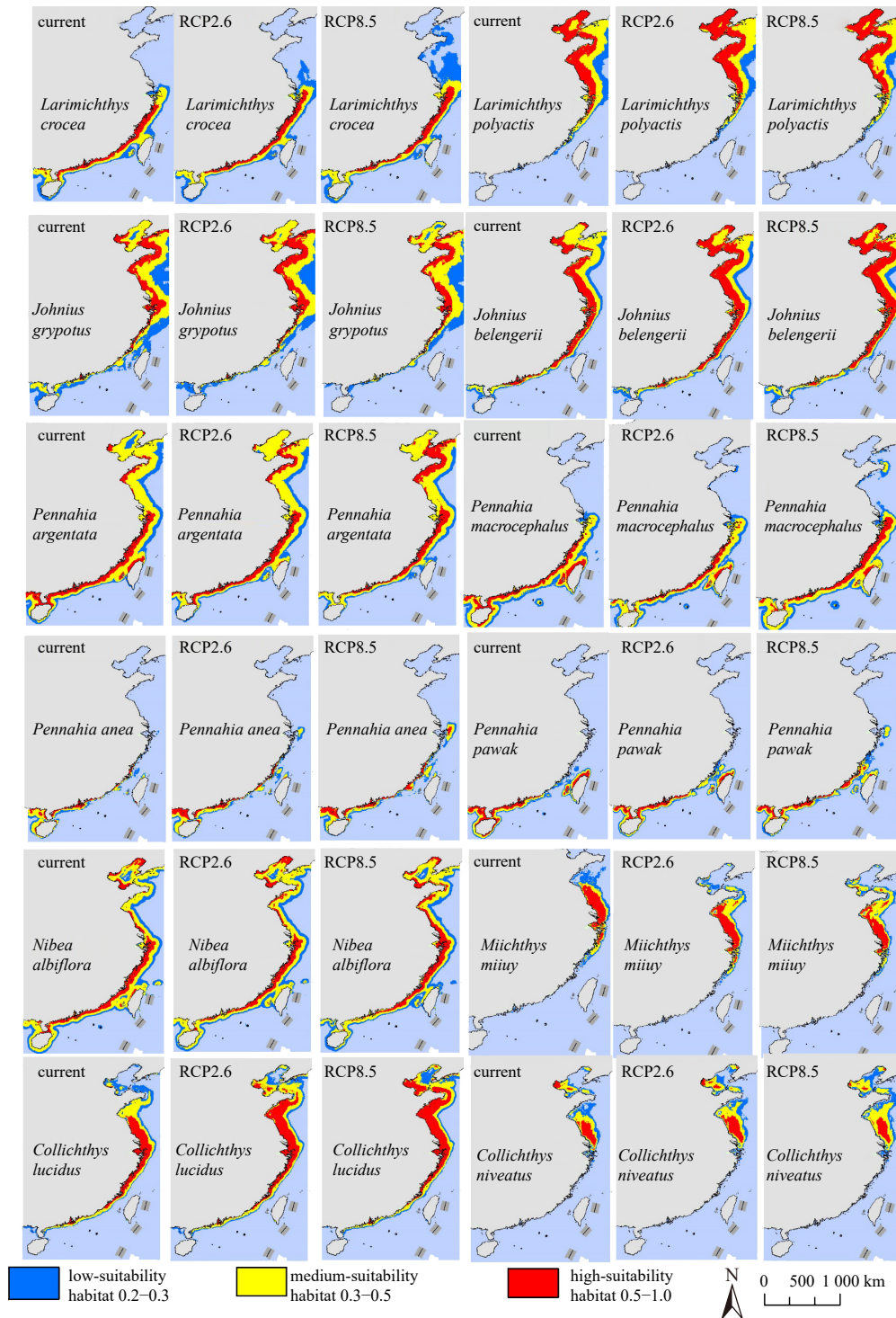


Fig. 3. Prediction of current habitat distribution and future habitat distribution for the 2041–2060 period based on the RCP2.6 and RCP8.5 climate change scenarios.

Zhujiang River Estuary, and the Taiwan Strait, while the species richness increased significantly in the northern Yellow Sea and the central Bohai Sea. The species richness of Sciaenidae in northern waters increased more under the RCP8.5 scenario than the RCP2.6 scenario. We selected 16 of the 53 marine type national aquatic germplasm resources reserves which included Sciaenidae as main conservation targets. Details of the results are shown in Table 6. The Donghai Largehead Hairtail and Qiansan Island national aquatic germplasm reserves both have the

highest richness of Sciaenidae. The high climate change sensitivity of individual reserves is evidenced by their proportion of shared species, like the Changdao Abalone and Sea Urchin national aquatic germplasm reserve. The results also show that the changes in the richness and area change rates under climate change are independent of each other, with only two reserves showing decreases in both their richness and area change rates (the Donghai Largehead Hairtail and Rudong Razor Clam/Surf Clam national aquatic germplasm reserves). In the case of *L.*

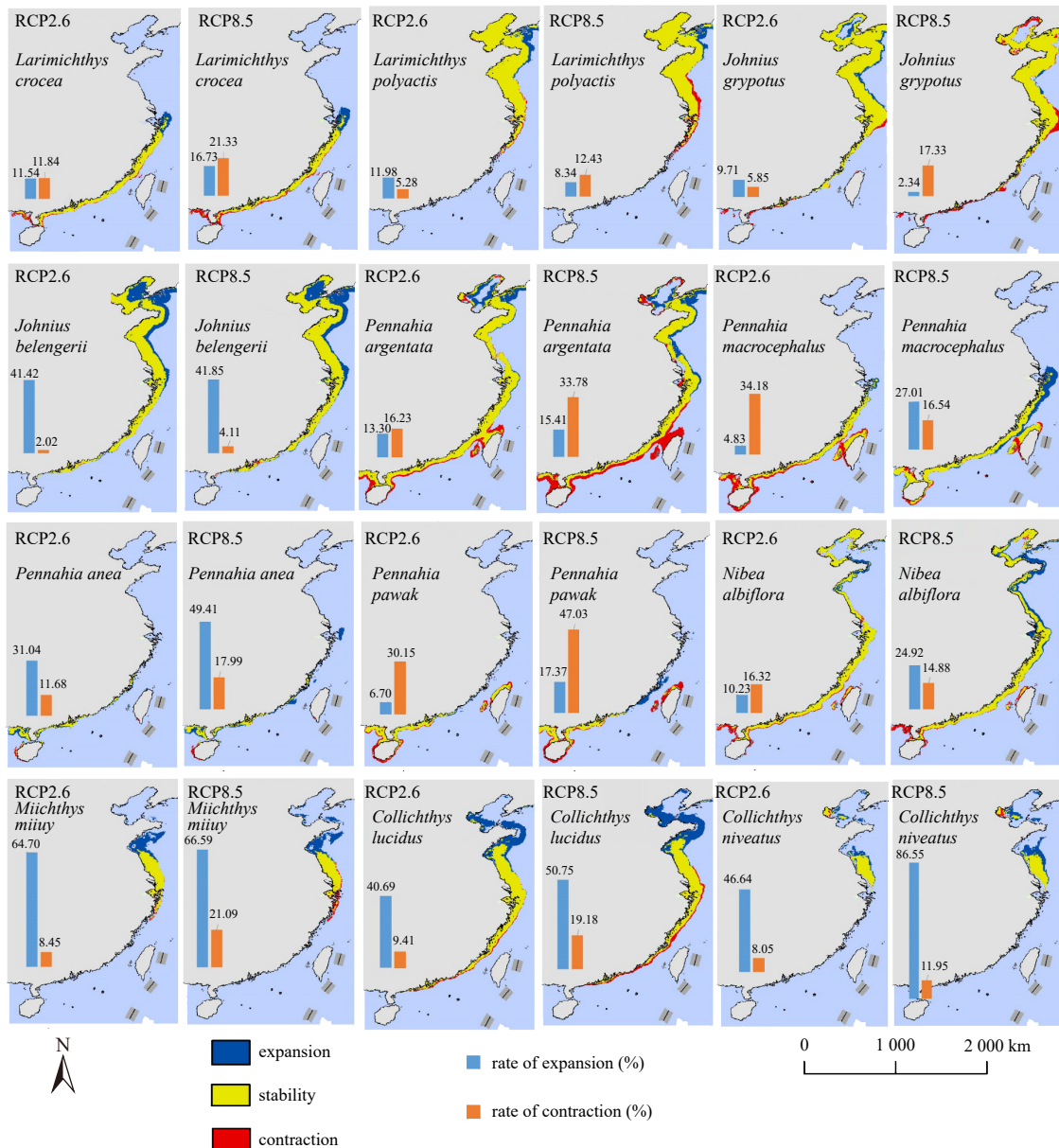


Fig. 4. Changes of potential Sciaenidae habitats under the RCP2.6 and RCP8.5 climate scenarios.

polyactis, for example, there are 12 protected aquatic germplasm resource areas, and the changes in the habitat area distribution under the climate scenario are shown in Fig. 6. Overlaying the *L. polyactis* national aquatic germplasm resource reserves, located in the Lüsi fishing grounds in the southwestern Yellow Sea (red boxed area in Fig. 6), showed that the richness of Sciaenidae increased in its triangular area and significantly increased its trapezoidal core area near the shoreline; moreover, it increased more under the RCP8.5 scenario.

4 Discussion

4.1 Effect of environmental factors on fish distribution and model validity

Temperature has a strong influence on fish growth, development, and reproductive processes, as well as on fish migration, community structure, resources, and habitat distribution. Salinity also plays an important role in fish growth, development, and

habitat distribution (Chen et al., 2019; Han et al., 2019; Jiang et al., 2006). Some studies have concluded that sea temperature is an important environmental factor that affects the temporal and spatial distribution of fish in different oceanic fish habitat prediction studies (Costa et al., 2021; Chen and Chen, 2016; Yang et al., 2022; Zhang et al., 2020a). In addition, studies in the coastal waters of China have shown that the distribution of marine fish such as lizardfish mainly depends on the average annual benthic sea temperature, owing to climate change (Wang et al., 2021). The results of this study also show that temperature was the dominant environmental factor affecting the distribution of fish habitats. The assessment of the habitat of *C. lucidus* in the Changjiang River Estuary concluded that salinity affects its distribution, and that habitat suitability is higher in the highly saline waters of the northern branch of the Changjiang River Estuary (Yang et al., 2014), which is consistent with the conclusion that salinity plays a decisive role in the potential distribution of the genus *Collichthys* in this study. Dissolved oxygen is an important environment-

Table 4. Spatial pattern changes in potential Sciaenidae habitats under different future climate change scenarios

	Current		RCP2.6 scenario					
	The total area/km ²	The total area/km ²	Rate of change/%	Expansion area/km ²	Rate of expansion/%	Stability area/km ²	Contraction area/km ²	Rate of contraction/%
<i>Larimichthys crocea</i>	152 799.37	152 344.99	−0.30	17 638.58	11.54	134 706.41	18 092.96	11.84
<i>Larimichthys polyactis</i>	263 894.87	281 568.34	6.70	31 606.44	11.98	249 961.90	13 932.97	5.28
<i>Johnius grypotus</i>	377 112.31	391 667.46	3.86	36 606.16	9.71	355 061.31	22 051.01	5.85
<i>Johnius belengerii</i>	249 780.74	348 187.63	39.40	103 448.92	41.42	244 738.71	5 042.03	2.02
<i>Pennahia anea</i>	66 919.24	79 876.62	19.36	20 773.98	31.04	59 102.64	7 816.60	11.68
<i>Pennahia argentata</i>	413 733.32	401 618.63	−2.93	55 031.74	13.30	346 586.89	67 146.43	16.23
<i>Pennahia macrocephalus</i>	215 773.19	152 440.02	−29.35	10 417.43	4.83	142 022.59	73 750.60	34.18
<i>Pennahia pawak</i>	112 929.37	86 448.11	−23.45	7 571.59	6.70	78 876.53	34 052.84	30.15
<i>Nibea albiflora</i>	293 061.36	275 219.02	−6.09	29 985.04	10.23	245 233.98	47 827.38	16.32
<i>Miichthys miiuy</i>	62 502.89	97 658.16	56.25	40 436.52	64.70	57 221.64	5 281.25	8.45
<i>Collichthys lucidus</i>	205 666.85	269 987.48	31.27	83 678.00	40.69	186 309.48	19 357.37	9.41
<i>Collichthys niveatus</i>	46 941.92	65 053.44	38.58	21 891.38	46.64	43 162.06	3 779.85	8.05

	Current		RCP8.5 scenario					
	The total area/km ²	The total area/km ²	Rate of change/%	Expansion area/km ²	Rate of expansion/%	Stability area/km ²	Contraction area/km ²	Rate of contraction/%
<i>Larimichthys crocea</i>	152 799.37	145 773.49	−4.60	25 559.12	16.73	120 214.37	32 585.00	21.33
<i>Larimichthys polyactis</i>	263 894.87	253 112.89	−4.09	22 008.69	8.34	231 104.21	32 790.66	12.43
<i>Johnius grypotus</i>	377 112.31	320 600.11	−14.99	8 837.48	2.34	311 762.63	65 349.68	17.33
<i>Johnius belengerii</i>	249 780.74	344 062.53	37.75	104 544.05	41.85	239 518.48	10 262.26	4.11
<i>Pennahia anea</i>	66 919.24	87 944.91	31.42	33 061.66	49.41	54 883.25	12 035.99	17.99
<i>Pennahia argentata</i>	413 733.32	337 727.88	−18.37	63 755.62	15.41	273 972.25	139 761.06	33.78
<i>Pennahia macrocephalus</i>	215 773.19	238 367.67	10.47	58 280.74	27.01	180 086.94	35 686.25	16.54
<i>Pennahia pawak</i>	112 929.37	79 443.02	−29.65	19 620.20	17.37	59 822.82	53 106.55	47.03
<i>Nibea albiflora</i>	293 061.36	322 457.45	10.03	73 018.74	24.92	249 438.71	43 617.82	14.88
<i>Miichthys miiuy</i>	62 502.89	90 946.36	45.51	41 622.47	66.59	49 323.89	13 179.00	21.09
<i>Collichthys lucidus</i>	205 666.85	270 594.07	31.57	104 380.71	50.75	166 213.36	39 453.48	19.18
<i>Collichthys niveatus</i>	46 941.92	81 962.18	74.60	40 628.05	86.55	41 334.13	5 607.79	11.95

Table 5. Centroid shifts of potential Sciaenidae habitats under different future climate change scenarios

Species	Centroid latitude			Degree of northward shift		Shifts distance/km		Shifts rate/(km·(10 a) ^{−1})	
	Current	RCP2.6	RCP8.5	RCP2.6	RCP8.5	RCP2.6	RCP8.5	RCP2.6	RCP8.5
<i>Larimichthys crocea</i>	24.62°N	25.52°N	26.13°N	0.90°	1.51°	108.59	181.66	24.68	41.29
<i>Larimichthys polyactis</i>	35.80°N	36.18°N	36.40°N	0.39°	0.60°	46.20	72.53	10.50	16.48
<i>Johnius grypotus</i>	33.70°N	34.37°N	34.41°N	0.68°	0.71°	81.07	85.18	18.43	19.36
<i>Johnius belengerii</i>	32.74°N	33.89°N	34.07°N	1.14°	1.33°	137.03	159.36	31.14	36.22
<i>Pennahia anea</i>	22.14°N	22.46°N	23.23°N	0.32°	1.09°	38.07	130.98	8.65	29.77
<i>Pennahia argentata</i>	29.05°N	30.95°N	31.83°N	1.90°	2.78°	227.50	334.06	51.70	75.92
<i>Pennahia macrocephalus</i>	23.51°N	24.73°N	24.87°N	1.22°	1.36°	145.94	163.67	33.17	37.20
<i>Pennahia pawak</i>	21.72°N	22.05°N	22.49°N	0.32°	0.77°	38.63	92.43	8.78	21.01
<i>Nibea albiflora</i>	29.36°N	30.92°N	31.37°N	1.57°	2.02°	187.92	241.98	42.71	55.00
<i>Miichthys miiuy</i>	31.99°N	33.50°N	34.01°N	1.50°	0.51°	180.52	242.00	41.03	55.00
<i>Collichthys lucidus</i>	29.77°N	32.32°N	33.27°N	2.54°	3.49°	305.25	419.08	69.38	95.25
<i>Collichthys niveatus</i>	34.39°N	34.77°N	34.96°N	0.37°	0.57°	44.96	68.30	10.22	15.52
Mean				1.07°	1.40°	128.47	182.60	29.20	41.50

al factor affecting the distribution of fish, and it has been shown that dissolved oxygen is an important factor affecting the spatial distribution of fish in the Leizhou Bay, the near-shore waters in south-central Zhejiang, and the Changjiang River Estuary (Zeng et al., 2019; Zhang et al., 2020c; Ma et al., 2020). Dissolved oxygen also played a decisive role in the distribution of most of the Sciaenidae species in this study, and its permutation importance was the highest for the three species of the genus *Pennahia*. The output results of the MaxEnt model for predicting the distribution of fish habitats were compared with existing fish records (Chen et al., 2021; Liu et al., 2020; Wang et al., 2016).

The distribution of *L. polyactis* was similar to that reported in a study in the Changjiang River Estuary (Zhang et al., 2020b), and more precise compared to global-scale studies (Cheung et al., 2009). Also, the distribution of *L. polyactis* in China was closer to land than that reported in the previous study (Liu et al., 2020). The distribution estimate may benefit from higher environmental parameter resolution and a more accurate distribution database. The output of the MaxEnt model for predicting the distribution of fish habitats was compared with the literature, and the predicted results were consistent with the actual distribution, which verified the validity and accuracy of the model for predict-

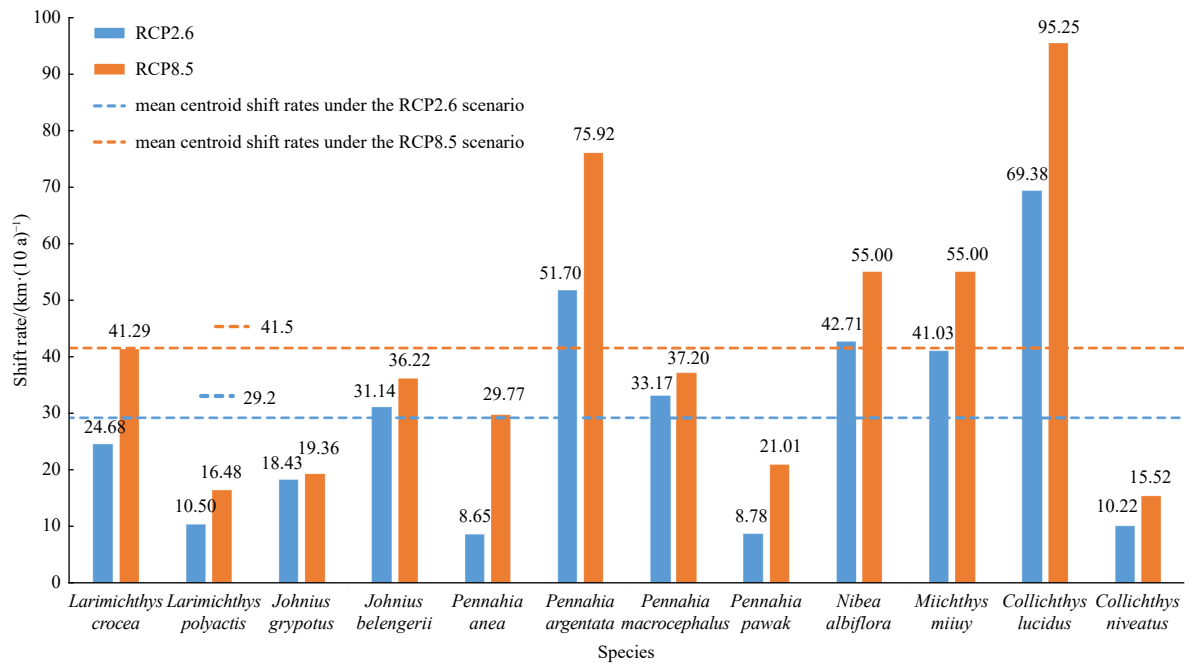


Fig. 5. Centroid shift rates of potential Sciaenidae habitats under different future climate change scenarios.

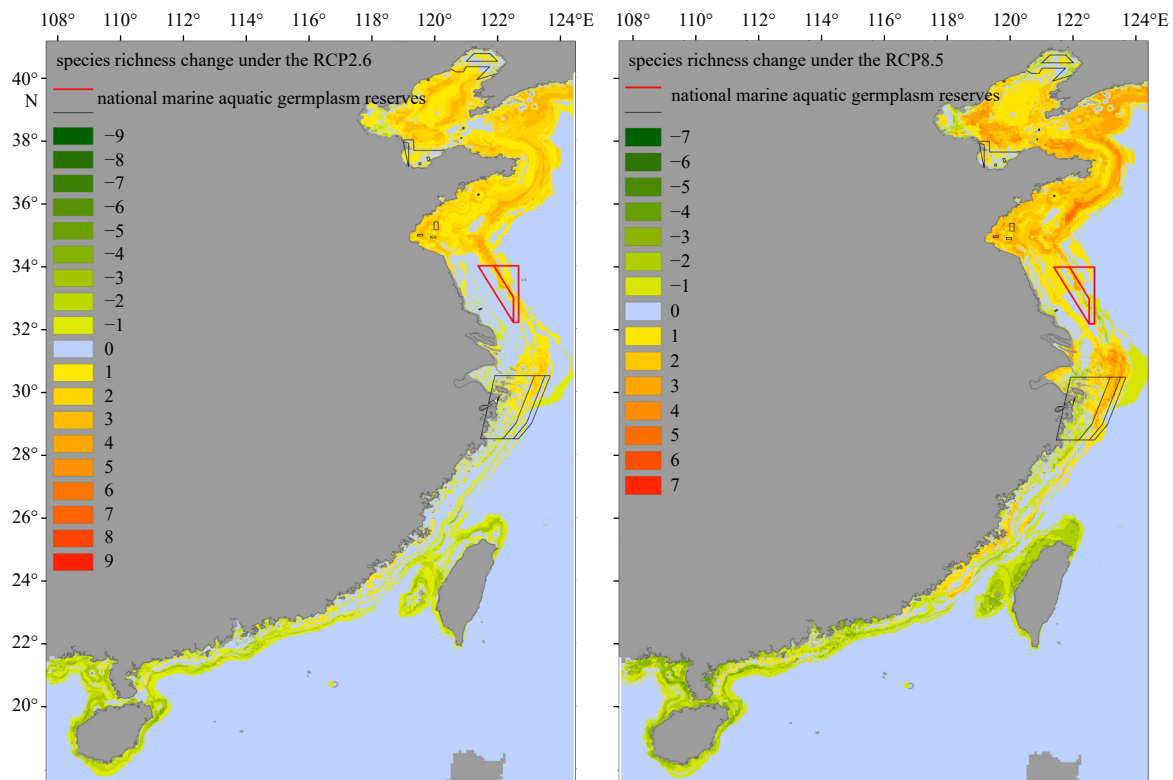


Fig. 6. Species richness changes of Sciaenidae under different future climate change scenarios. The black and red framed areas are the *Larimichthys polyactis* national aquatic germplasm reserves.

ing the potential distribution of Sciaenidae.

However, there was still some uncertainties in the model projections. Firstly, using a single Maxent model was likely to cause high uncertainty, and ensemble SDMs were used in more and more studies to reduce uncertainty in the recent years (Segurado and Araujo, 2004; Thuiller et al., 2019). Secondly, the species interaction, and adaptability of species to environment, and fish-

ing efforts also should be considered in future studies in order to reduce uncertainty.

4.2 Changes in fish habitats and shifts patterns under two climate change scenarios

In global-scale studies of climate change impacts on the distribution of marine fish, the distribution centroid and polarward

Table 6. Changes in marine-type aquatic germplasm reserves of the Sciaenidae under climate scenarios

Name	Current	RCP2.6 scenario			RCP8.5 scenario		
	Richness of Sciaenidae	Richness of Sciaenidae	Shared species	Mean change rate of habitat area/%	Richness of Sciaenidae	Shared species	Mean change rate of habitat area/%
1	8	8	8	12.4	8	8	14.5
2	5	7	5	28.6	7	5	28.6
3	2	4	2	50.0	3	2	33.3
4	8	8	8	-7.8	8	8	-3.6
5	9	7	7	-28.8	7	7	-31.9
6	9	9	9	22.0	11	9	92.6
7	5	7	5	28.6	7	5	28.6
8	7	7	7	17.1	7	7	10.4
9	8	8	8	-6.6	9	7	-11.1
10	4	4	4	12.5	4	4	137.5
11	3	5	3	55.0	4	3	43.8
12	6	6	6	75.9	6	6	6.7
13	5	7	5	443.0	7	5	251.4
14	8	8	8	-8.8	7	7	-14.3
15	6	7	6	341.7	7	6	341.7
16	4	6	4	35.1	6	4	35.1

Note: 1: Ningde Guanjing Yellow Croaker Breeding National Aquatic Germplasm Reserve; 2: Haizhou Bay Razor Clam National Aquatic Germplasm Reserve; 3: Changdao Abalone and Sea Urchin National Aquatic Germplasm Reserve; 4: Jiangjia Shazhu Snail National Aquatic Germplasm Reserve; 5: Shangxiachuan Island Chinese Lobster National Aquatic Germplasm Reserve; 6: Donghai Largehead Hairtail National Aquatic Germplasm Reserve; 7: Qiansan Island National Aquatic Germplasm Reserve; 8: Lüsi Fishing Grounds Little Yellow Croaker and Butterfish National Aquatic Germplasm Reserve; 9: Xiangshan Japanese Spanish Mackerel National Aquatic Germplasm Reserve; 10: Changdao Scorpionfish National Aquatic Germplasm Reserve; 11: Qianliyan National Aquatic Germplasm Reserve; 12: Haizhou Bay Chinese Prawn Aquatic Germplasm Reserve; 13: Liaodong Bohai Bay Laizhou Bay National Aquatic Germplasm Reserve; 14: Rudong Razor Clam/Surf Clam National Aquatic Germplasm Reserve; 15: Rizhao Chinese Prawn National Aquatic Germplasm Reserve; 16: Shanhaiguan Coastal Area National Aquatic Germplasm Reserve.

distribution boundaries of most species have been found to shift towards the poles, with the median range shift rates of 1 066 species of marine fish and invertebrates ranging from 45 km to 59 km per decade (Cheung et al., 2009). Recent model projections suggest global distributional shifts rates of tens to hundreds of kilometre per decade for marine species under future climate scenarios, with higher rates under higher climate emission scenarios (Jones and Cheung, 2015; Worm and Lotze, 2021). Recent assessments have further clarified that the average rate of poleward movement of marine species is 59.2 km/(10 a) (43.7–74.7 km/(10 a)), which is higher than the rate of this study (Lenoir et al., 2020). In this study, the habitats of 12 fish species changed under both RCP2.6 and RCP8.5, with the overall centroid latitude migrating from lower to higher latitudes and the total area of some fish habitats decreasing. These changes were more pronounced under the RCP8.5 climate scenario, consistent with the direction of shifts in global-scale studies (Cheung et al., 2009; Jones and Cheung, 2015; Worm and Lotze, 2021). Under RCP2.6 and RCP8.5, the Sciaenidae species of China migrate northward at mean shift rates of 29.20 km/(10 a) and 41.50 km/(10 a), respectively, which are also within the range of the shifts rates in the abovementioned global-scale studies, indicating that this study has good credibility (Cheung et al., 2009).

In regional-scale research on the impact of climate change on the distribution of marine fish, the distribution centroids of 28 pelagic fish in the Northeast Pacific continental shelf were found to migrate toward the polar regions at an average rate of (30.1 ± 2.34) km per decade under the influence of climate (Cheung et al., 2015). The distribution of 686 marine species on the North American continental shelf are predicted to shift along the coastline toward increasing latitudes under climatic change, and the magnitude of the shifts is much greater under the RCP8.5 scenario than under the RCP2.6 scenario (Morley et al., 2018). Fifteen

of the 36 fish species in the Atlantic North Sea would shift in response to climate change and most species would shift northward, with some southward-migrating species likely caused by inconsistent patterns of change in spatial temperature gradients between the southern and northern North Sea owing to North Atlantic warming (Perry et al., 2005). The study area is located in the offshore regions of China, and the results of Sciaenidae fishes are consistent with the trends in shifts direction and rate in the northern hemisphere.

Studies on predicting the impacts of climate change on marine fishes in Chinese waters are relatively few and limited to studies on single species or in specific waters (Zhang et al., 2020b; Wang et al., 2021). Researchers used ensemble species distribution models to find that the habitat distribution of *Sebastes schlegelii* will be reduced under climate change, and the greatest impact will be under the RCP8.5 scenario, under which habitat distribution will be reduced by 45% by 2100 (Chen et al., 2021b). The findings of that study are consistent with the results of the current study that the high emission climate scenario will have a more significant impact on the potential habitat area of Sciaenidae (Chen et al., 2021b). In addition, it has been shown that the Changjiang River Estuary has high suitability for the distribution of five ichthyoplankton fishes: climate change favors the expansion of the habitat of *Coilia mystus*, while the habitat ranges of the other four species decreased and they are predicted to migrate northward, resulting in a decrease in the diversity of these five species in this area (Zhang et al., 2020b). The results of this study are consistent with the expansion or reduction of fish habitat areas owing to climate change, and all the habitats in this study shifted northward (Zhang et al., 2020b). However, it has also been found that the distribution centroids of 34 warm-water fish species in the Yellow Sea will move southward at shift rates of (2.96 ± 1.29) km/(10 a) and (3.20 ± 1.94) km/(10 a) under the

RCP2.6 and RCP8.5 climate scenarios, respectively. This is likely owing to the topography, fluctuations in coastal currents, warm currents, cold water masses, and overfishing in the study area (Zhu et al., 2020). Moreover, a related study in China found that 22 species of fishes distributed in China's coastal waters would shift 110–206.5 km under climate change, which is smaller than the 38.07–419.08 km range reported in this study. This difference may be related to the selection of different fish species for the study (Hu et al., 2022). The northward shifts of the potential fish habitat under climate change in this study are contrary to the aforementioned results, and the shift rate of each fish species was relatively high, probably owing the differences in the study scale and species. Unlike studies on single species or local waters, this study investigates the effects of climate change on the distribution patterns of 12 common economically important Sciaenidae species in the coastal waters of China, which not only improves the understanding of the current distribution, but also predicts the effects of climate change on these distribution patterns. The results of the above-mentioned studies also indicate the comprehensiveness and accuracy of this study (Cheung et al., 2009; Chen et al., 2021b; Zhang et al., 2020b). In addition, the shrinkage of the *P. macrocephalus* and *P. pauwak* was prominent among the 12 species under climate change, while the expansion of the *M. miu* and *C. niveatus* habitats was also significant, probably owing to the fact that the main habitats of the former two species are located south of the Changjiang River Estuary and their temperature and dissolved oxygen ecological niches are narrower. Therefore, the areas of water conforming to the required ecological niches will be reduced with climate change. The latter two species are distributed north of the Changjiang River Estuary. Their temperature and dissolved oxygen ecological niche are wider, and climate change will cause an increase in the areas included these ecological niches.

4.3 Climate shelters and management recommendations

The map of species richness shows that the richness of Sciaenidae in the southern seas of China has decreased significantly, while the richness of Sciaenidae in the northern sea of China has increased, and will probably become a refuge for the family under climate change. In a study of global fish responses to climate change, it was found that global biological richness increased significantly on the polar side of species distribution ranges and decreased significantly on the equatorial side (Hastings et al., 2020). Moreover, local species extinction commonly occurs in sub-polar, tropical, and semi-enclosed waters (Cheung et al., 2009). The richness of Sciaenidae declined significantly in the tropical sea, with the most pronounced decline in the Beibu Gulf, probably because of its tropical location and the isolation of the barrier caused by its geographical position, making it more difficult for fish to migrate northward to seek refuge under climate change (Burrows et al., 2014). At this stage, the number and area of marine national aquatic germplasm resource reserves are relatively small, and there are regional differences in the establishment of protected areas (Bohorquez et al., 2021; Sheng et al., 2019). According to our results, the rate of change in the overall reserves for species' habitats is increasing. This may be consistent with the pattern that more aquatic germplasm reserves are established in the north than in the south in China and they are larger in size (Sheng et al., 2019). Therefore, in the future, fishing activities in waters such as the Beibu Gulf, where the richness will decrease significantly, needs to be strictly controlled. Both the Donghai Largehead Hairtail and Rudong Razor Clam/Surf Clam national aquatic germplasm reserves have high sensitivity to cli-

mate change and more attention should be paid to the potential challenges and opportunities for fishery managers in the context of the changing distribution of economic species. For sea areas such as the Jiaodong Peninsula, where the richness of Sciaenidae will increased, measures such as adjusting the scope of the original aquatic germplasm resource reserve should be adopted to increase marine protection. For example, the aquatic germplasm resource reserve for *L. crocea* in the Lüsi fishing ground to the north of the Changjiang River has supervised and expanded the reserve area for aquatic germplasm resources to adapt to changes in the distribution and diversity of Sciaenidae species.

5 Conclusions

The results of the present study reveal the dominant environmental factors influencing the distribution of Sciaenidae, the current and future distribution patterns of Sciaenidae and their response to climate change. Climate change will have a huge impact on the distribution of fish habitats. The results were analyzed in the context of existing aquatic germplasm reserves as a scientific basis for future fish conservation and management. Some reserves should pay more attention to the potential challenges and opportunities for fishery managers in the context of the changing distribution of economic species.

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